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DENSITY-DEPENDENT HABITAT UTILIZATION OF GROUNDFISH AND THE IMPROVEMENT OF RESEARCH SURVEYS

by

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ABSTRACT

We examine how the geographical distribution of species changes in response to changes in overall population size, as estimated from VPA. We identify the following patterns of changes. First, a population may respond to a change in population size by a proportional increase throughout its range. This is our null hypothesis since it involves no density-dependent response in habitat utilization. This pattern was observed in North Sea haddock and American plaice from the Grand Banks of Newfoundland. The second response is range extension in which the population increases relatively more in marginal habitats. The third response is a relatively greater increase in the prime habitat. This response was observed in North Sea cod. We also observed cases where the VPA estimates were correlated with research surveys from one region but not others, which indicated functional stock subdivision.

Résumé

Nous examinons comment la distribution géographique des espèces varie en fonction des changements de la taille globale de la population, selon les estimations APV. Nous observons les modes de changement suivants. Premièrement, une population peut répondre à une variation, de sa taille par une augmentation proportionnelle dans toute son aire. Il s'agit là de notre hypothèse nulle car elle ne fait intervenir aucune réponse liée à la densité pour l'utilisation de l'habitat. Ce processus a été observé chez l'aiglefin de la mer du Nord et chez la plie canadienne des bancs de Terre-Neuve. La seconde réponse est l'extension de l'aire, où la population augmente relativement plus dans les habitats secondaires. La troisième réponse est une augmentation relativement plus grande de l'habitat principal. Cette dernière réponse a été observée chez la morue de la mer du Nord. Nous avons également observé des cas où il y avait corrélation entre les estimations APV et les résultats de campagnes de recherches pour une région donnée, mais non pour d'autres, ce qui révèle une subdivision fonctionnelle du stock.

1 Introduction

We ask the following question: "How does the distribution of animals change as their abundance change?"

The approach taken here is to develop simple models to describe the density-dependent habitat utilization and to apply these models to a number of species. The emphasis here is on simple graphical procedures. Formal hypothesis testing is a straightforward extension of the work presented here.

We use two types of estimates of abundance typically available for many marine and freshwater fisheries. First, we consider estimates of the total numbers of animals in the population in each year. Such estimates are typically available from VPA's. We denote such estimates at time t by N_t. Second, we consider local estimates of density at specific locals or within small regions. These are typically obtained from research surveys. We denote such estimates of site i at time t by $n_{i,t}$. We are concerned here with the relationship between N_t and $n_{i,t}$ over time, i.e how does local population density change as a function of the total population abundance.

2 Data and Analysis

The response of local population density, $n_{i,t}$, to the total population abundance, as estimated from a VPA, was described by the following model:

$$n_{i,t} = \alpha_i N_t^{\beta_i}.$$

This model is fit to each site, in our case North Sea fishing squares, using data for all years. The geographical variation in $\hat{\beta}_i$, and the response of $\hat{\beta}_i$ to the mean local density over time was used to test ecological hypotheses.

We use data from the English groudfish surveys of the North Sea for the periods 1977 to 1988 to estimate local density, $n_{i,t}$. The surveys from each fishing square were pooled for the estimates. The estimates of total abundance in each year were from the VPA analyses from the latest ICES assessments.

The estimates of the local population response, $\hat{\beta}_i$, were calculated by two methods. First, we transformed the data by $\log(x + \frac{1}{2})$, and then used an ordinary least squares regression to estimate the β_i's. The factor of $\frac{1}{2}$ is needed because of the presence of zeros. Myers and Pepin (1986) found this to give a reliable estimate of the slopes unless there were two many zero's present. To test the reliability of this simple approach, some of the slopes were estimated using GLIM without transforming. We assumed a Poisson error model with overdispersion. Similar results were obtained in both cases, so only the first will be presented here.

3 Models and Results

3.1 Site Invariant Response (the Null Hypothesis)

Our simplest model is that local density should change in proportion to the change in total abundance throughout the range of a population. If the site invariant response hypothesis is correct then $\beta_i = 1$ for all sites i (Fig. 1). Fig. 1 near here

The local response of local population density is not a function of local population density for haddock (Fig. 2). The local population response did not show any geographical pattern. Thus, haddock appears to be consistent with a site invariant response. Using a different approach, Myers (1987, unplublished results) showed that American plaice on the Grand Banks of Newfoundland was consistent with a site invariant response. Fig. 2 near here

3.2 Site Variable Response - Habitat Saturation

If the best habitats are filled first, then the slopes β_i should be greater than 1 for sites with low mean density, and less than one for sites with high mean density. Thus, this hypothesis can be tested by regressing the β_i versus the mean population density at site i. This type of response would be expected in populations with fixed territory size.

None of the groundfish species examined were consistent with this response.

3.3 Site Variable Response - Population Concentration

If a population tends to concentrate as population increases then we expect that the estimate of the slopes of the local population response, $\hat{\beta}_i$'s, versus the mean local density averaged over time, $n_{i,\cdot}$. In this case we expect this regression to be positive. This type of behaviour does not seem consistent with published theories of habitat selection.

The local population response of age 1 cod is an increasing function of local population density. Thus, age 1 cod appears to become more concentrated as overall population density increases. Fig. 3 near here

3.4 Response if there are separate populations

In the above discussion we have assumed that our estimate of total population in year t, N_t, represents one population. It may be that there is more than one population present which changes size independently. In this case we would not expect the response as predicted as above. By plotting the geographical distribution of the correlation of the VPA with the local density it is possible to locate the region that is best correlated with total abundance.

In the previous examples, the data under study probably pertained to a single interbreeding stock or population. It is quite common for a stock complex to be managed as a single unit even when there is evidence to the contrary. In such cases the interpretation of research survey and catch data must be decomposed so that they are relevant to individual stocks if possible. This process is illustrated by whiting. Although whiting occurs throughout the North Sea, there is evidence that there are separate stocks in the eastern and western parts of the North Sea. The catch however, mainly comes from the western half of the North Sea. The result is that there is very little correlation of the VPA with the research surveys index. However, if one examines the correlations of the research surveys with the VPA on a smaller scale, a clear pattern emerges. The VPA is correlated with research surveys from the west, but not in general from the east (Fig. 4). Fig. 4 near here

4 Conclusions

- The geographical structure of the research survey catches is critical to examine when interpreting survey results. It is seen for whiting that the VPA is providing information only one part of the stock complex.

- The local population response is often not uniform over the North Sea. In particular, cod shows strong density-dependent habitat utilization. A survey that only covered part of the range would be nonlinearly related to the true changes in stock abundance.

- Surveys should cover the entire range of a stock.

5 Acknowledgments

We thank John Dann for helping to compile the data, and John Pope and John Shepherd for helping clarify our ideas.

6 References

Myers, R. A. and P. Pepin. (1986). The estimation of population size from research surveys using regression models. International Commission for the Exploration of the Sea C.M.1986/D:9.

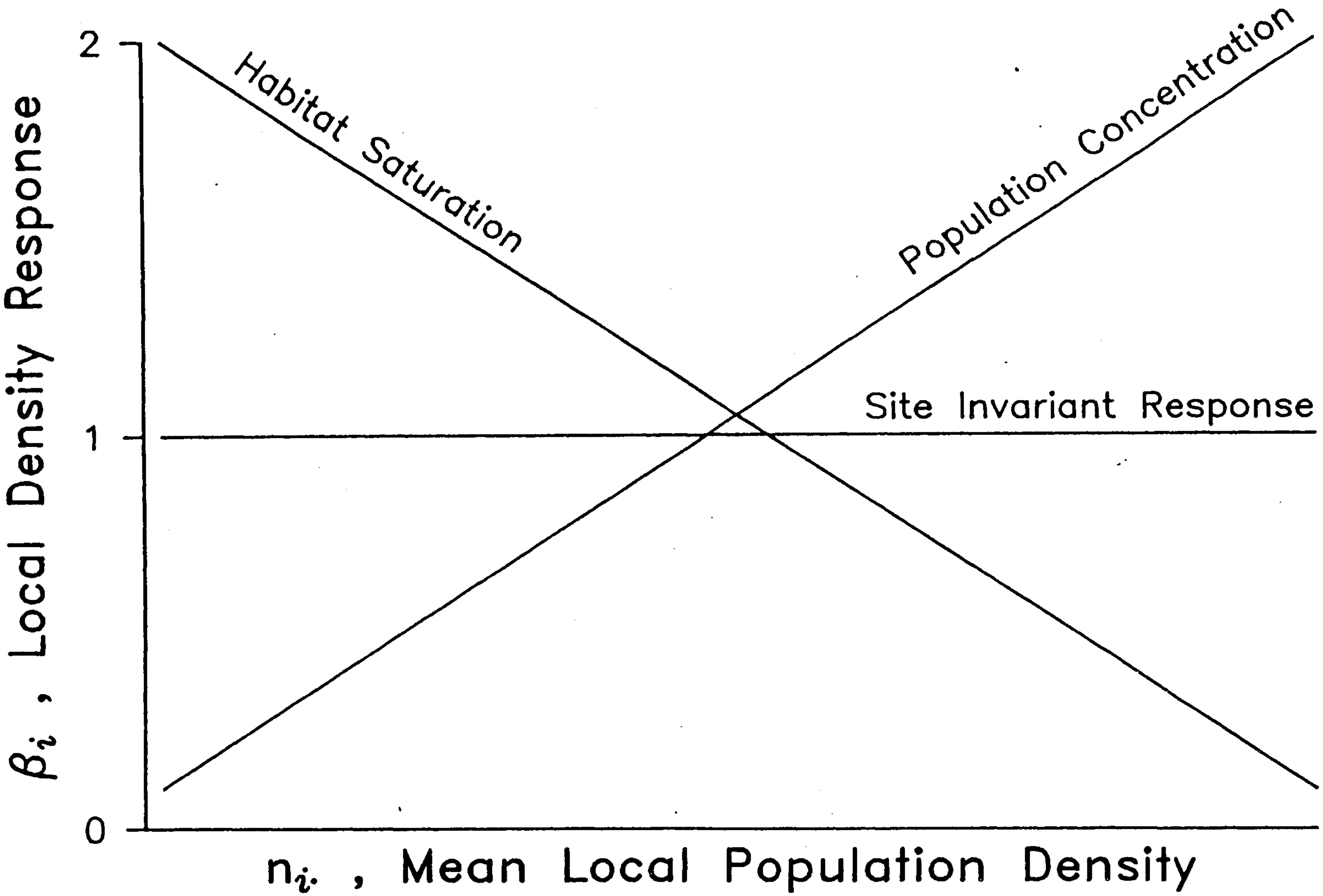

Fig. 1 The predicted response in local density to overall changes in abundance for the three main models presented.

Fig. 2a. The mean local density for age 1 haddock from the English groundfish surveys. The area of the circles is proportional to mean local density.

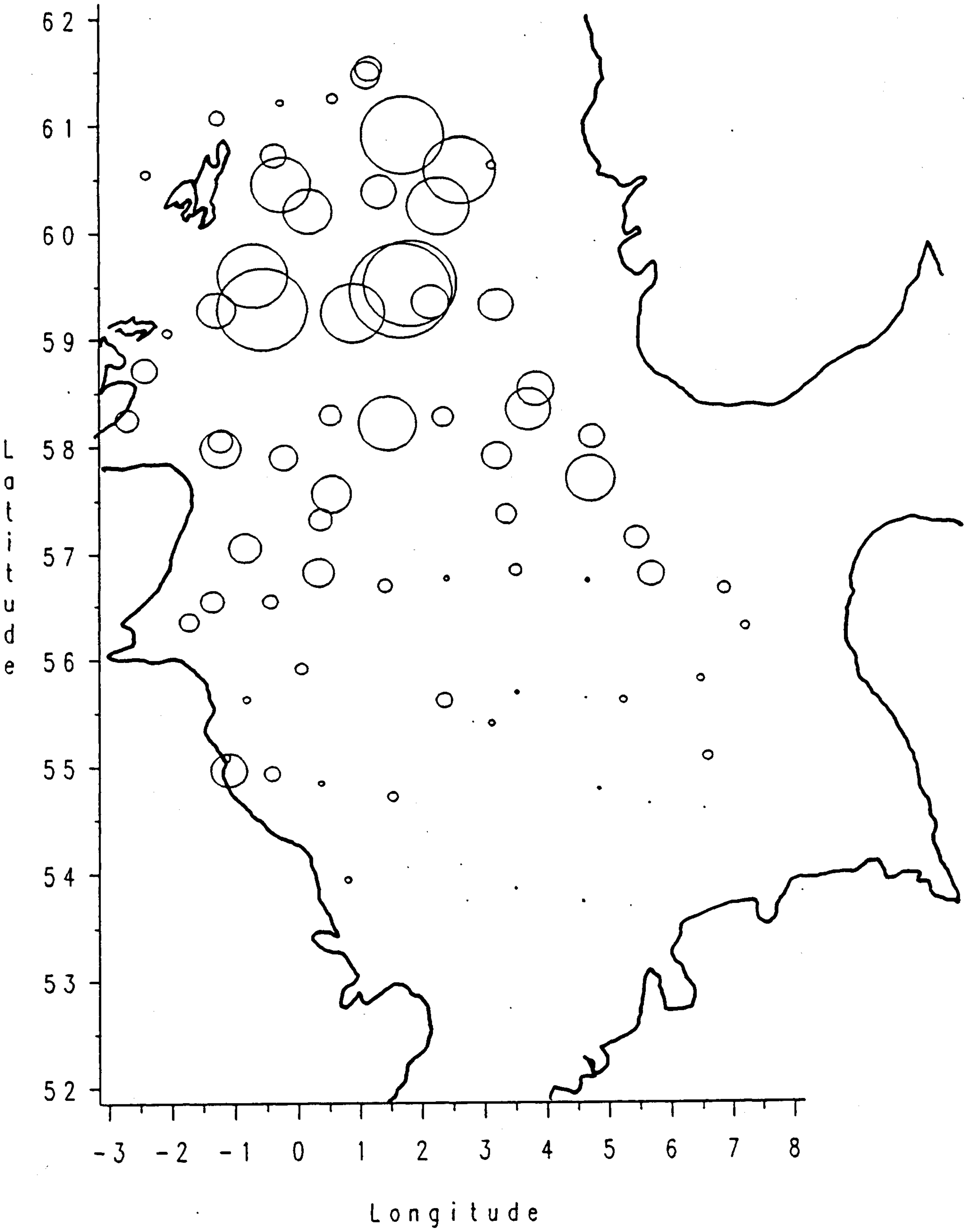

Fig. 2b. The geographical distribution of the local response to changes in overall abundance, $\hat{\beta}_i$. The area of the circles is proportional to $\hat{\beta}_i$; dashed circles are negative slopes.

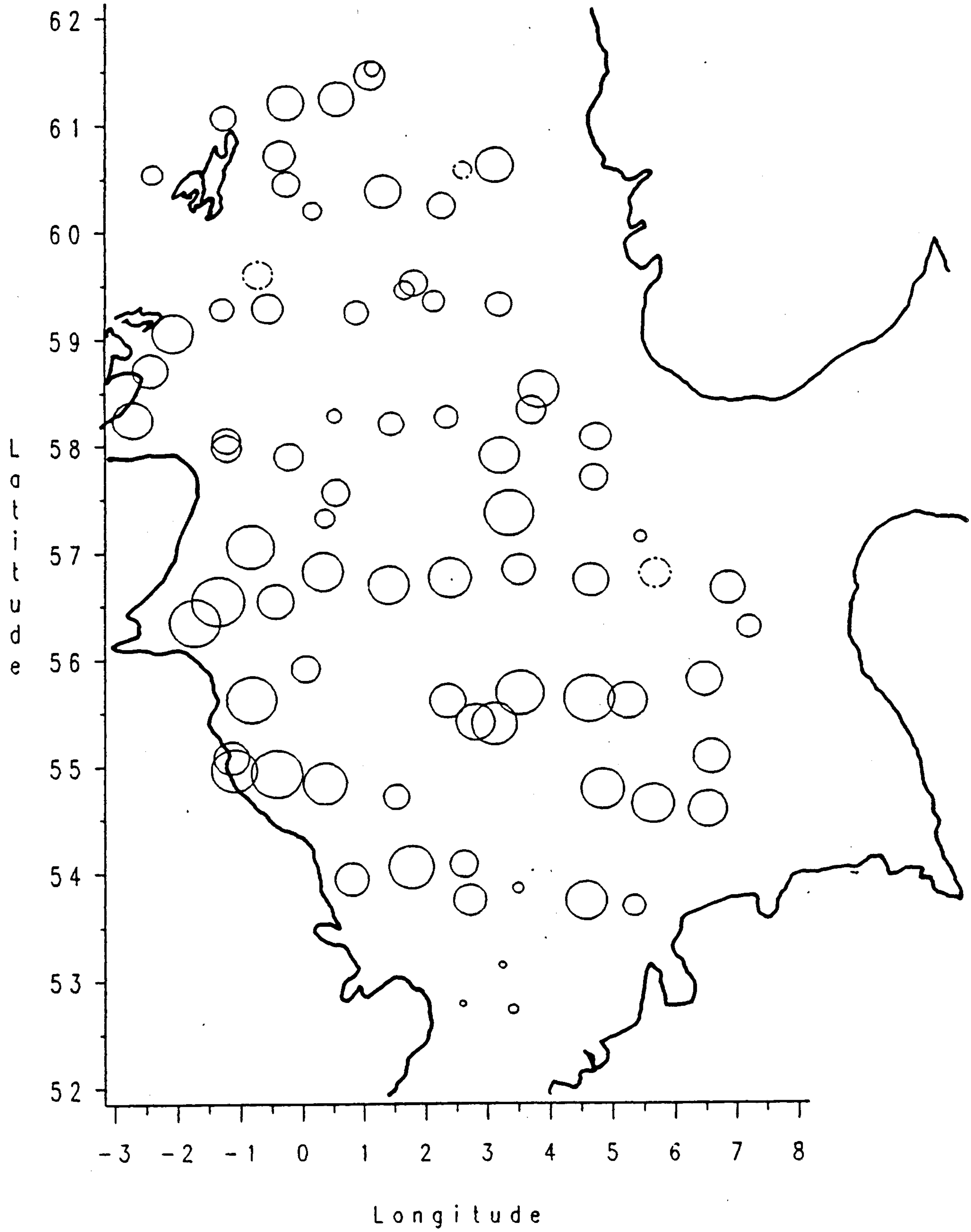

Fig. 2c. The local response to changes in overall abundance, $\hat{\beta}_i$, versus the mean of the log. of local population density for age 1 haddock. The area of the circles is inversely proportional to the standard error of the slope. Thus, small circles are from regions with few samples and should be given less weight than larger circles. This data is consistent with a site invariant response.

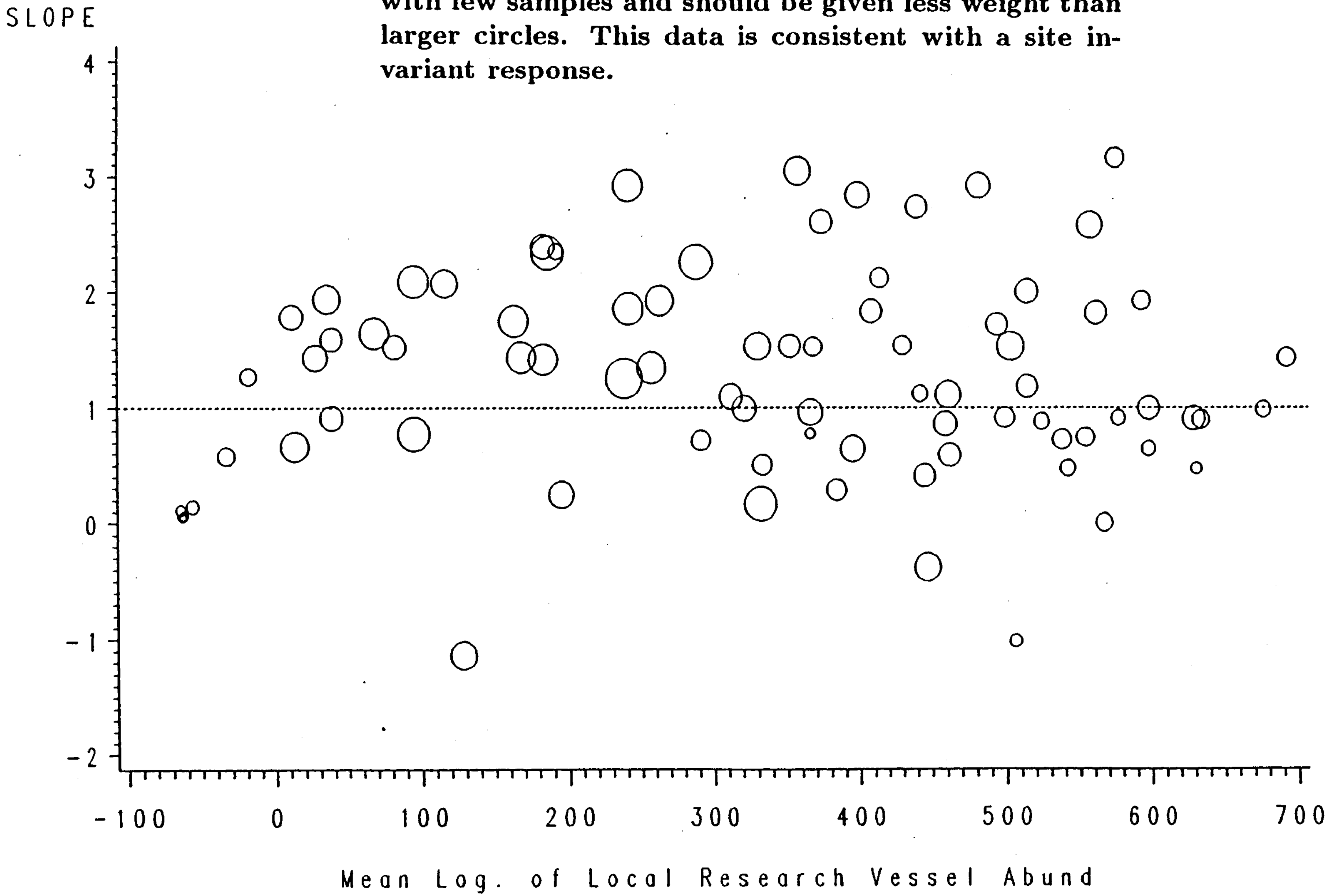

Fig. 3a. The mean local density for age 1 cod from the English groundfish surveys. The area of the circles is proportional to mean local density.

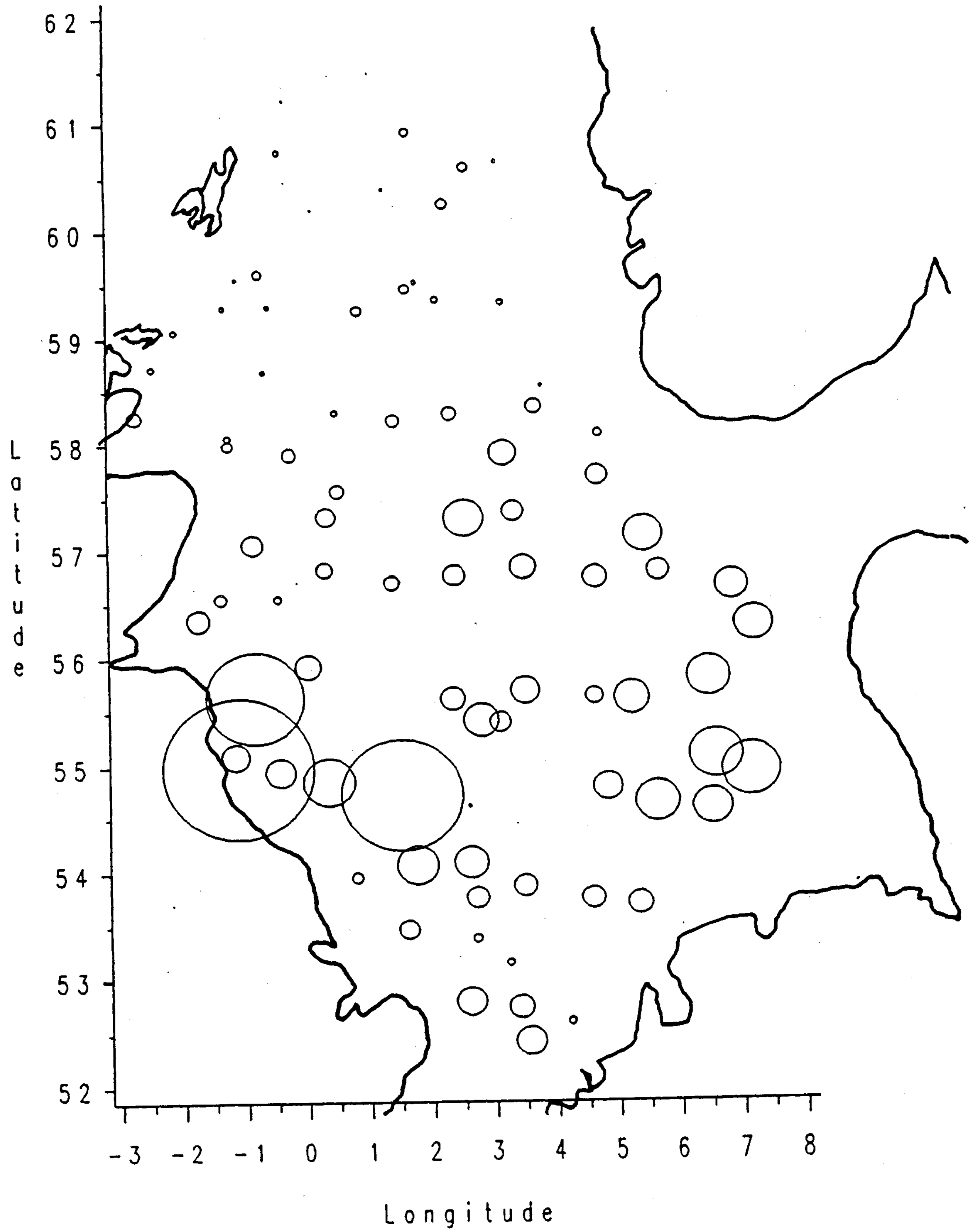

Fig. 3b. The geographical distribution of the local response to changes in overall abundance, $\hat{\beta}_i$. The area of the circles is proportional to $\hat{\beta}_i$; dashed circles are negative slopes.

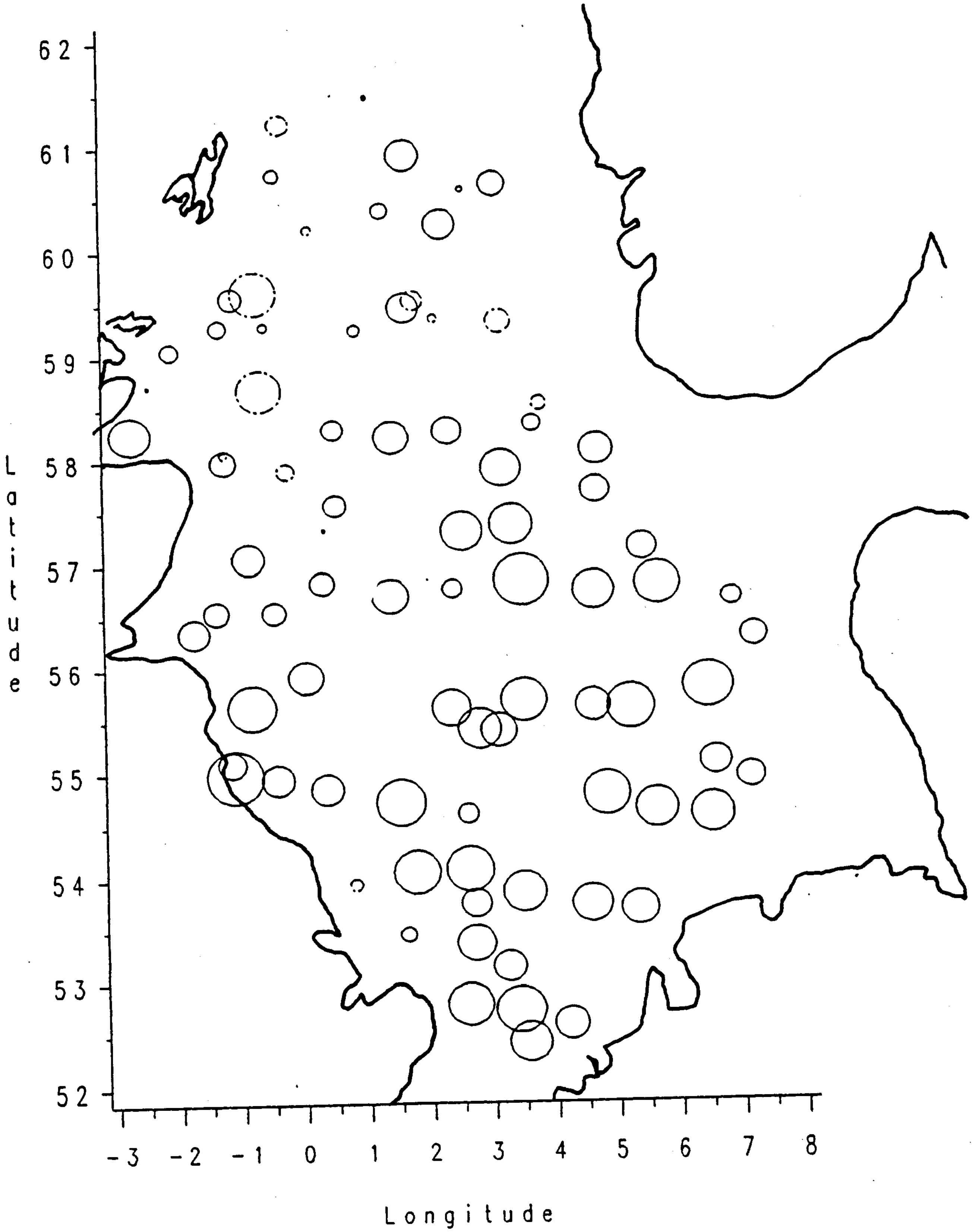

Fig. 3c. The local response to changes in overall abundance, $\hat{\beta}_i$, versus the mean of the log. of local population density for age 1 cod. The area of the circles is inversely proportional to the standard error of the slope. Thus, small circles are from regions with few samples and should be given less weight than larger circles. This data is consistent with a population concentration response.

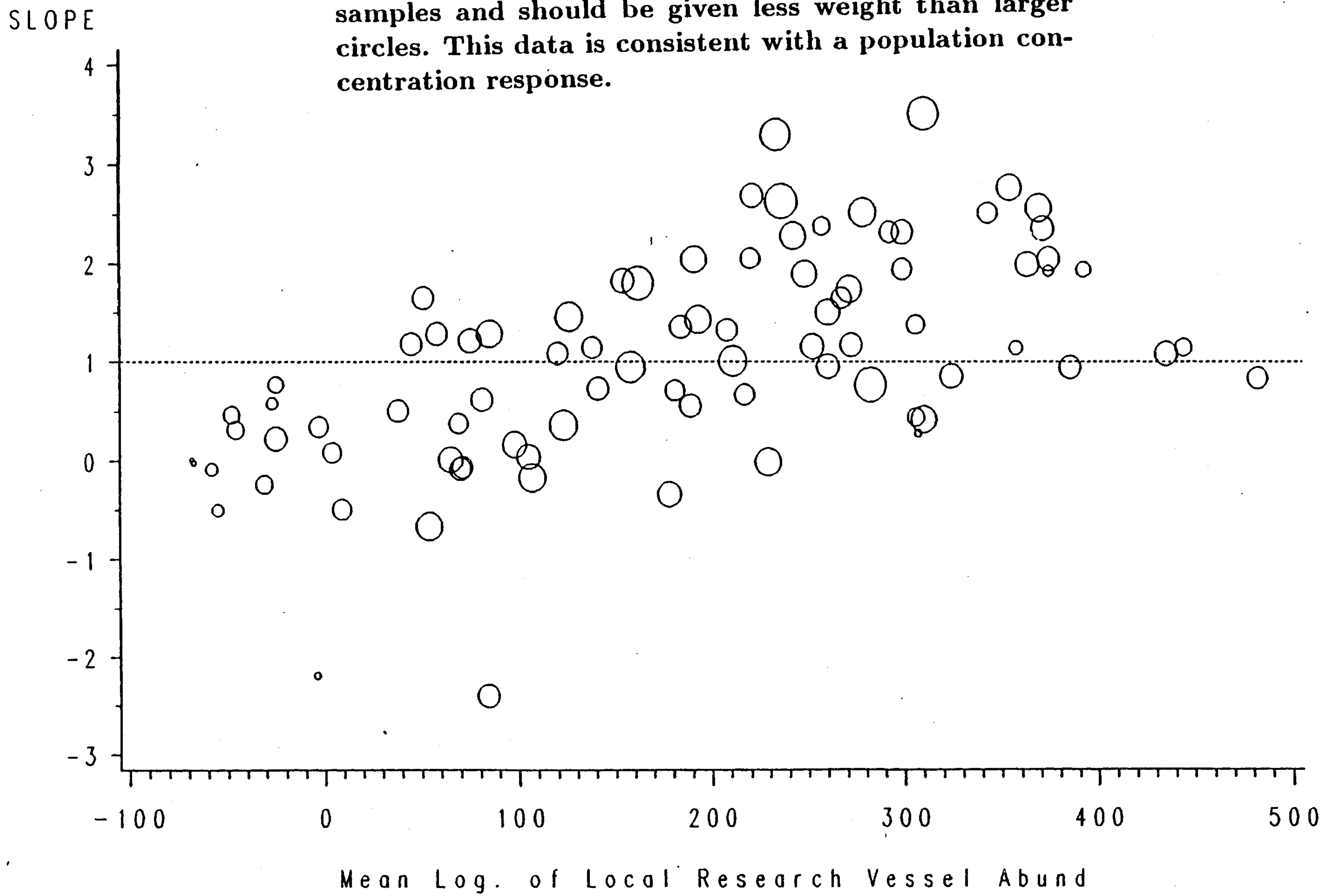

Fig. 4a. The mean local density for age 1 whiting from the English groundfish surveys. The area of the circles is proportional to mean local density.

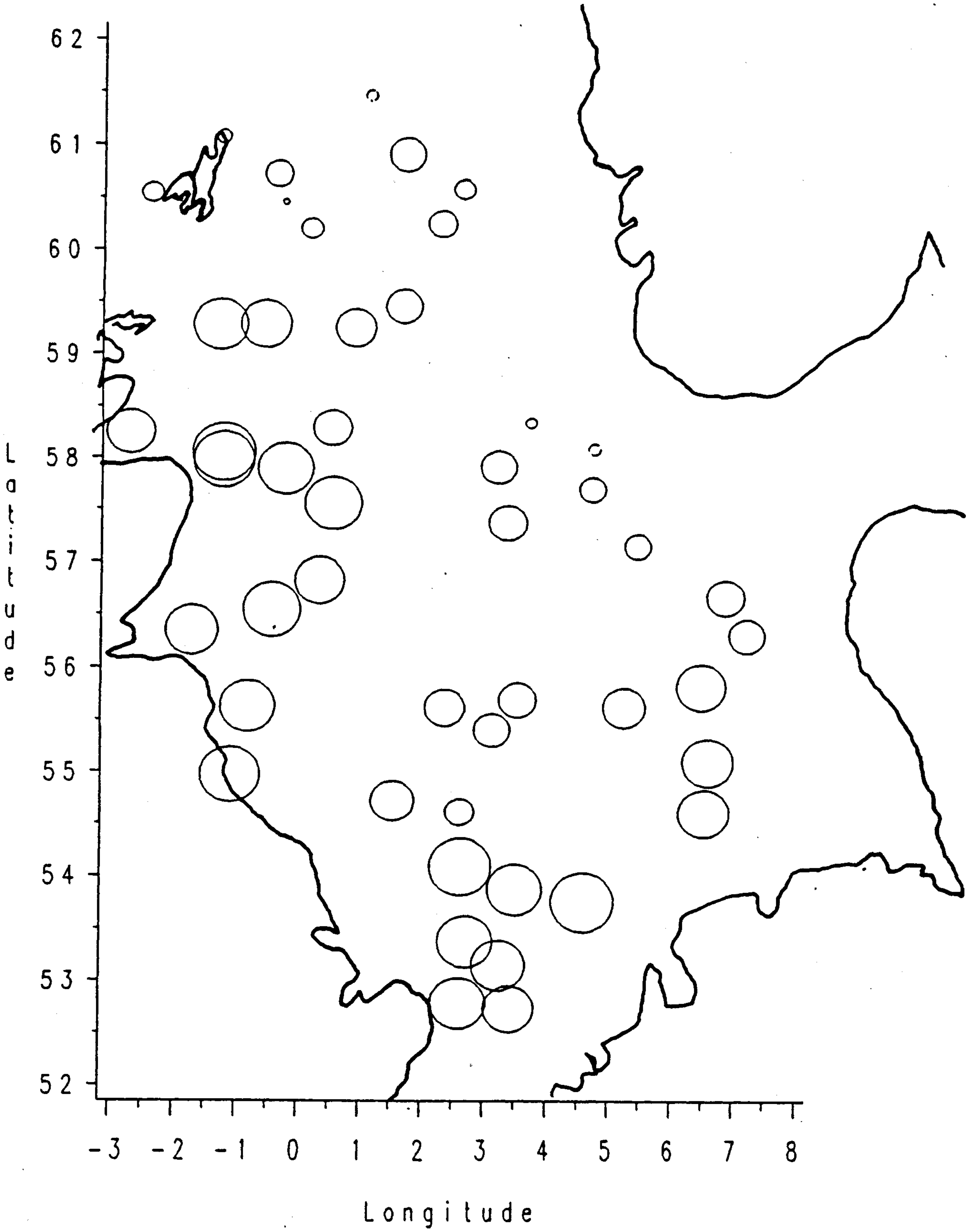

Fig. 4b. The geographical distribution of the correlation between the VPA estimates of total abundance and the local research survey estimates for age 2 whiting. The area of the circles is proportional to the correlation; dashed circles are negative slopes.

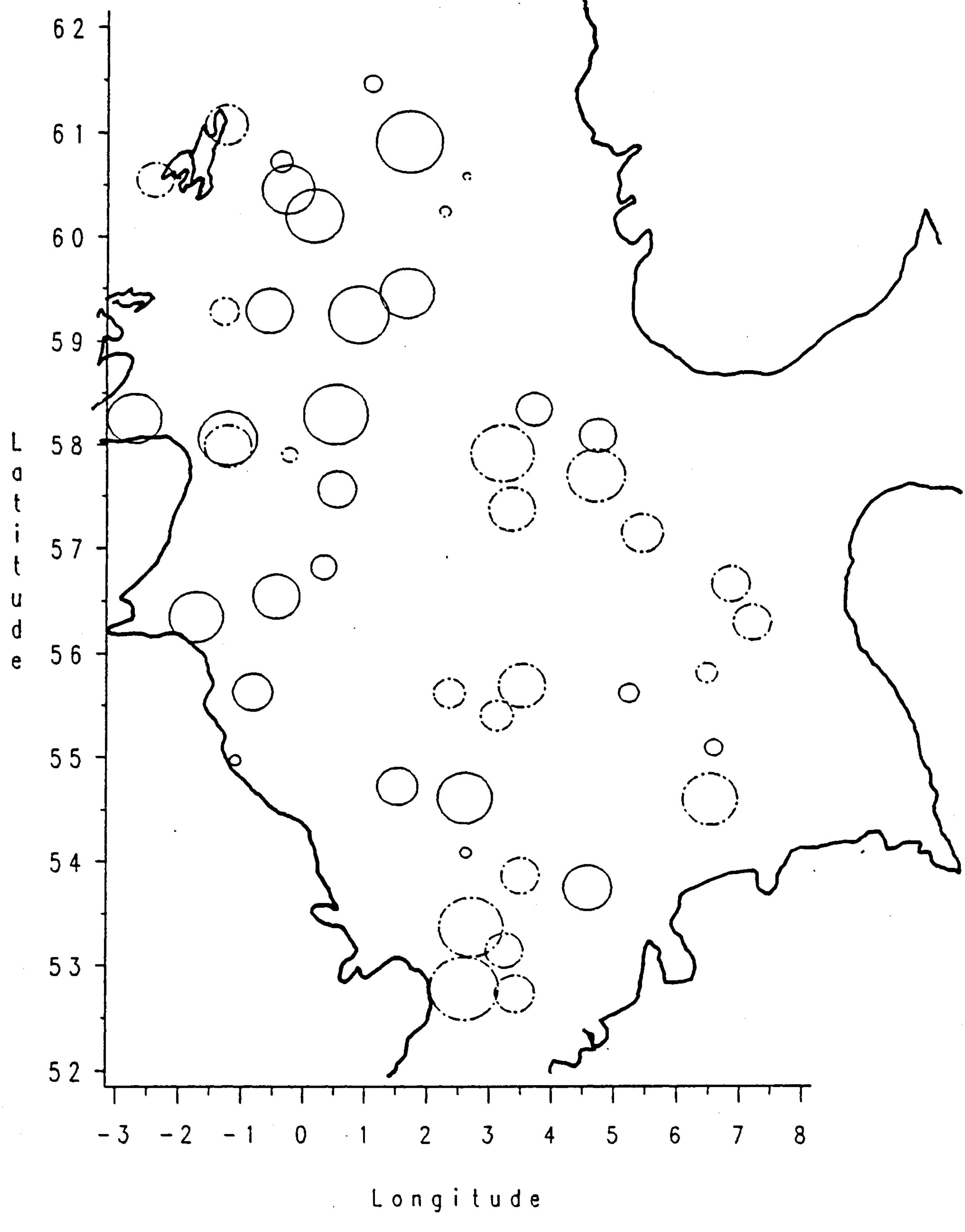

Fig. 4c. **The correlation between the VPA estimates of total abundance and the local research survey estimates for age 2 whiting versus the the mean of the log. of local population density. area of the circles is inversely proportional to the standard error of the slope.**